

## Interspecific Variation in Hunting Behavior of *Pepsis grossa* (Fabricius) and *Pepsis thisbe* Lucas (Hymenoptera: Pompilidae): A field study

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**Abstract.**—Field studies were conducted on encounters between the spider wasps *Pepsis grossa* (Fabricius) and *P. thisbe* Lucas, and females of their host spider, *Aphonopelma steindachneri* (Ausserer) (Theraphosidae), in Big Bend National Park, Texas. Females of *P. grossa* were significantly larger than those of *P. thisbe*. Number of eggs found in ovarioles of *P. grossa* and *P. thisbe* ranged from 6–14 and 3–12, with a mean of 11.3 and 8.4, respectively. Behavioral acts comprising hunting behavior of both species included antennation of a spider's burrow (BA), evicting spiders from their burrow (EVB), initial approach and antennation of spider (AA), moving away and grooming (MG1), attack and paralysis (AP), moving away/grooming (MG2), drinking behavior (DB), burial of spider and egg deposition (BO), and closure of the burrow entrance (BC). Antennae of most wasps made initial contact with the forelegs or palps of a spider. During AP, wasps typically grasped leg 3 or 4 of the host before inserting their stings. Most wasps of *P. grossa* (78%) inserted their sting into the intersegmental membrane between the sternum and coxa 2 of the spider; 88% of *P. thisbe* females chose a site between the sternum and coxa 1. Only 33 and 26% of *P. grossa* and *P. thisbe*, respectively, drank fluids from a spider's mouth or from sting insertion site (LB). *Pepsis thisbe* required significantly more time (mean: 129.1 min) to complete all behavioral acts of hunting than *P. grossa* (mean: 101.4 min). Wasps were successful in paralyzing spiders in all observed encounters, and no spider attempted to attack a wasp.

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Aculeate spider wasps of the genus *Pepsis* (Hymenoptera: Pompilidae) include at least 133 species varying in size from >60 mm to <12 mm in length (Vardy 2000). Most members of this genus have been referred to as tarantula hawk wasps because females selectively hunt mygalomorph spiders of the family Theraphosidae (Cazier and Mortenson 1964, Punzo and Garman 1989, Vardy 2002). They paralyze and store these spiders (hosts) in underground nests (Williams 1956, Punzo and Ludwig 2005) as a food source for their carnivorous larvae (Punzo 1994a). They occur throughout the New World, from the United States and West Indies, south to Patagonia (Hurd 1952, Vardy 2000).

*Pepsis grossa* (Fabricius 1798) and *P. thisbe* Lucas (1895) are large, long-legged wasps and are conspicuous components of the

arthropod fauna of desert regions in the southwestern United States and northern Mexico (Hurd 1952, Vardy 2000, Punzo, 1994b, 2006a). In Big Bend National Park (BBNP; Brewster County, Texas, USA), females of these two species, as well as *P. mildei* Stål (1844) selectively hunt and paralyze the large theraphosid spider, *Aphonopelma steindachneri* (Ausserer 1929) which they use as a host for their developing larvae (Punzo 2005a).

Adult wasps feed on nectar which is obtained from flowers of a variety of plants (Evans and West-Eberhard 1970, Punzo 2000, 2006a). In BBNP, where ambient temperatures in late spring and summer may exceed 43 °C, it is not uncommon for females to fly over considerable distances during daylight hours in search for flowers and host spiders (Punzo 1994b, Schmidt

2004). It is important for females to obtain adequate amounts of required nutrients because insect flight places high metabolic demands on insects (Nation 2002).

Females of *Aphonopelma steindachneri* (Ausserer), like other spiders of this genus, excavate burrows (or occupy abandoned rodent burrows) where they remain for most of their lives (Baerg 1958, Gabel 1972, Punzo 2007a). Females seize prey that approaches close to the burrow entrance. Adult males actively wander over the ground surface during the mating season when they search for conspecific females (Punzo 2000, 2007b).

Female *Pepsis* wasps initiate their search for suitable spider hosts after mating (Punzo 1994b, 2006a,b). They typically fly over the ground and are thought to detect occupied spider burrows at a distance using visual and/or odor cues. They intermittently interrupt flight by landing on the ground and walk rapidly over the surface, tapping the ground surface frequently with their antennae as they search for spider burrows (Kurczewski and Kurczewski 1968). When a suitable spider burrow is located, the female wasp typically stops at the entrance and taps the edge of the opening with her antennae (burrow antenation, BA). After a variable period of time, she cuts through the silk covering over the burrow entrance with her mandibles, enters the burrow, and usually forces the spider out of its burrow and onto the surface (EVB, eviction behavior). Male theraphosids are usually encountered as they move about searching for food and mates (Minch 1979, Punzo 2005b, 2007b). Unlike burrow-dwelling females, males of the genus *Aphonopelma* from desert regions usually seek shelter within or under rock crevices, or under surface debris (Smith 1994, Punzo and Henderson 1999).

A specific sequence of behavioral acts are exhibited once a spider has been forced to the ground surface. These acts comprise the overall attack behavior of *Pepsis* wasps

found in the tropics and desert regions of the southwestern United States (Petrunkevitch 1926, 1952, Cazier and Mortenson 1964, Punzo and Garman 1989, Punzo 1991, 1994b, 2005a,c). A female wasp typically approaches the spider and touches its body surface with her antennae (approach and antenation, AA) (Punzo and Garman 1989). In some cases, the spider does not move away, although it may twitch one of its forelegs or raise its palps off the ground (Punzo 2007b). In other instances, tactile stimulation by a wasp elicits a threat posture from the spider which elevates the anterior legs and exposes its fangs (Petrunkevitch 1952, Punzo 1994b). However, the spider rarely strikes at the wasp, although if presented with another insect (cricket, etc.) it typically strikes quickly, seizing the insect and eating it. It has been suggested that chemosensory cues associated with the wasp's cuticle inhibit the spider's strike response (Punzo 2000).

Once a spider has been identified as a suitable host, the wasp moves a short distance away and exhibits grooming behavior by passing its antennae through the mandibles. This behavioral component is known as 'moving away and grooming' (MG1, Punzo 1991). After a few minutes, the wasp turns to face its host and then walks under the ventral body region of the spider. In response to this, spiders usually extend their legs, elevating their body off the ground. The wasp then grasps one of the spider's legs and quickly inserts its sting through the ventral body region into the prosomal nerve mass resulting in a rapid paralysis of the spider. This component of hunting is referred to as attack and paralysis (AP). Once a spider is immobilized, the wasp moves away and repeats the grooming sequence described above (MG2). It then returns to the spider and in some instances may either drink fluids from the spider's mouth cavity or drink spider hemolymph that leaks out of the puncture wound made by the insertion of the sting. This is known as drinking or

lapping behavior, DB (Punzo 2000). However, because DB does not occur in most encounters, the question arises as to what factor(s) may be responsible for its occurrence.

The paralyzed host is then dragged into the spider's burrow (or one excavated by the wasp) and a single egg is deposited on the ventral surface of the spider's abdomen (burial and oviposition, BO). The wasp then closes the burrow entrance (BC, burrow closure) using soil particles and small pebbles and flies off to search for another host.

Although behavioral acts of the hunting sequence have been studied, most observations are based on laboratory encounters between wasps and hosts (Punzo 1991, 1994b, 2007). Few detailed observations of encounters in the field have been described. In addition, there are a number of questions that remain. For example, when attacking a spider does a wasp exhibit any preference for grasping a particular leg? Are there specific sites on the spider's body where a wasp inserts its sting? How commonly does lapping behavior occur? Is there a preference for the site at which it occurs? Finally, are there interspecific differences associated with these behaviors? The present study was conducted in order to analyze hunting behavior of *P. grossa* and *P. thisbe* under natural conditions and to address these questions in these two sympatric species of wasps that are found in similar microhabitats in Big Bend National Park (BBNP), where both utilize *A. steindachneri* as a host.

#### DESCRIPTION OF GENERAL STUDY AREA

*Pepsis grossa* and *P. thisbe* occur throughout Big Bend National Park (BBNP) is located in Brewster County, Texas, and lies within the northern region of the Chihuahuan Desert. Its western, southern and eastern boundaries are bordered by the Rio Grande River. Climatic conditions range from arid to semiarid, with mean monthly

air temperatures ranging from 5.4°C in January to 33.8°C in August (US Dept. of Interior 2005). Annual rainfall is between 13.8–30.1 cm, depending on location and altitude, with 65–70% occurring from May through October (Parent 1996). Topography of the Park is diverse and includes gypsum formations, igneous rocks, and limestone deposits that provide different substrates including alluvial fans, gypsum flats, saline playas, siliceous and gypsum dunes, fine-textured basins, canyons, mountain ridges, and freshwater springs and seeps, all supporting a diverse plant fauna categorized within distinctive vegetative zones (Powell 1988).

#### MATERIALS AND METHODS

I conducted field studies over a 4-year period (2002–2005) within BBNP from May through September, when male wasps were establishing perch sites (territories) and females were searching for spiders. Adults of *P. grossa* and *P. thisbe* were observed within a 5-km radius of Tornillo Flat (TF; 29°01'N, 102°59'W), a site where both of these species are abundant, as well as their host spider, *A. steindachneri*, are abundant (Punzo 2000, 2007b). I had located and marked numerous occupied tarantula burrows during previous field studies in this area over the last 12 years ( $n = 946$ ). Females of *A. steindachneri* typically remain within a single burrow for most of their adult lives (Punzo, unpubl. data). As a result, I knew the locations of host spiders and concentrated my field observations at these burrow sites. Voucher specimens of wasps, wasp eggs, and spiders have been deposited in the invertebrate collection at BBNP.

Based on my knowledge of locations for burrows occupied by a female tarantula, I examined 148 burrows whose entrances had been closed from previously unobserved encounters with wasps to determine whether it contained a paralyzed host. During the course of this study I also monitored 96 burrows containing an adult



female spider, and observed 54 and 42 encounters between a wasp and spider for *P. grossa* and *P. thisbe*, respectively. Because encounters between a wasp and a male spider usually occur while the male is wandering over the ground surface, opportunities to witness such encounters occur far less frequent. Therefore, only encounters involving a female spider were used for analyses.

I observed all encounters at close range (1–2 m from combatants), and used a 35-mm Nikon FE2 camera to photograph some of the encounters. Encounters were observed during daylight and evening hours (0830–0200 h, Central Standard Time). At the end of each encounter (following burial, oviposition, and closure of the burrow) I collected the wasp with a sweep net and anesthetized it using a portable CO<sub>2</sub> cartridge. Once inactivated, I verified species identification and used a Unitron dissecting microscope fitted with an ocular micrometer to record body length and head capsule width. Although *Aphonopelma steindachneri* is the only theraphosid known to occur at the TF site (Smith 1994, Punzo 2007b), I opened each burrow to verify species identification of paralyzed spiders. I examined the body surface of paralyzed spiders with a dissecting microscope in order to locate the site where the wasp's sting had been inserted into the host during the paralyzation sequence. I also recorded the width of the carapace and total body length to the nearest 0.1 mm using a digital caliper. After removing the wasp's egg, I recorded weight of wasp eggs (to the nearest 0.01 mg) and spiders (to the nearest 0.01 g) using a portable electronic balance. Egg length and width were recorded to the nearest 0.01 mm using a dissecting microscope.

The site of the puncture wound could be readily identified by hemolymph that oozed out of the wound. Only data obtained for *P. grossa*, *P. thisbe* and the host *A. steindachneri* were used for analy-

ses. Another *Pepsis* wasp, *P. mildei* also occurs at TF, but is far less abundant (Punzo, unpubl. data). After measurements were recorded, each wasp was preserved in 70% ethanol for subsequent determination of number of eggs in ovarioles. Removal of wasps ensured that the same wasp was not involved in more than one encounter for the data set.

For each encounter I observed the general behavior of the wasp as it approached the burrow entrance and interacted with a spider, as well as the concomitant behaviors exhibited by the host. I recorded: (1) the amount of time required to complete the hunting sequence (from initial contact to closure of the burrow), as well as all behavioral components of hunting, using a stopwatch; (2) which spider leg was initially seized by the wasp as it attempted to insert its sting; (3) site at which wasp sting had been inserted into the body of the spider; and (4) whether or not lapping behavior occurred, and if so, where.

All statistical procedures followed those described by Sokal and Rohlf (1995). All data conformed to conditions of normality as assessed using a Bartlett's test for homogeneity of variances and a *G*-test for normality. Comparisons on means for morphometric data between the two species of wasps as well as for male and female spiders were tested using a *t* test. Differences between the proportion of burrows containing paralyzed males versus females, and frequency at which specific spider legs were grasped by a wasp during initiation of attack behavior, were tested using a Chi Square test ( $X^2$ ). Comparisons between time required by each wasp species to complete overall hunting sequence was tested using an analysis of variance (ANOVA), and a Scheffe *F* test was used for ad hoc comparisons between individual behavioral components of hunting.

## RESULTS

Of the 148 burrows whose entrances had been closed with soil (following previously

Table 1. Morphometric data on females of *Pepsis grossa* ( $n = 54$ ) and *P. thisbe* ( $n = 42$ ) and female host spiders, *Aphonopelma steindachneri* ( $n = 96$  females, 46 males) at Tornillo Flat, Big Bend National Park, Texas. Data from wasps and spiders examined from 2002 to 2005. Data expressed as means; values in parentheses represent ( $\pm$ SE). BL (body length); HCW (head capsule width); CW (cephalothorax width); BW (body weight); NEO (number of eggs found in ovarioles). Values in rows followed by a different letter are statistically significant ( $t$  tests;  $P < 0.05$ ).

	<i>Pepsis grossa</i>	<i>P. thisbe</i>	<i>A. steindachneri</i>	
BL (mm)	42.7a (2.4)	35.9b (1.7)		
HCW (mm)	4.9a (0.2)	3.9b (0.3)		
NEO	11.3a (2.4)	8.4b (0.7)		
			Males	Females
CW (mm)			13.4a (0.7)	15.2b (0.5)
BW (g)			6.8a (0.5)	10.8b (1.1)

unobserved encounters), 128 (87%) contained a paralyzed spider. Although the species of wasp responsible for the paralysis cannot be known unless the offspring is reared, 87 of these 128 burrows (68%) contained a female spider, and 32% held a male (Chi Square test:  $X^2 = 10.89$ ,  $P < 0.03$ ). Paralyzed male spiders ranged in weight from 5.2–6.4 g (mean:  $5.77 \pm 0.42$ ), while the range was 6.9–10.4 g (mean:  $7.94 \pm 0.37$ ) for females. For data obtained from observed encounters, female spiders paralyzed by *P. grossa* and *P. thisbe* had a mean weight of  $8.7 \pm 0.83$  g (range: 6.2–10.6) and  $7.7 \pm 0.64$  g (range: 5.7–10.7), respectively. Mean values for length, width, and weight for eggs of *P. grossa* were  $4.34 \pm 0.03$  mm,  $1.34 \pm 0.01$  mm, and  $7.14 \pm 0.31$  mg, as compared to  $4.29 \pm 0.05$  mm,  $1.24 \pm 0.02$  mm, and  $6.88 \pm 0.41$  mg for *P. thisbe*.

Morphometric data for wasps observed encountering spiders, as well as for hosts, are shown in Table 1. Concerning host spiders, based on width of cephalothorax ( $t = 3.04$ ,  $P < 0.05$ ) and body weight ( $t = 2.46$ ,  $P < 0.05$ ), females were significantly larger than males. For the two species of wasps, females of *P. grossa* were significantly larger than those of *P. thisbe*, based on body length ( $t = 3.35$ ,  $P < 0.05$ ) and head capsule width ( $t = 2.88$ ,  $P < 0.05$ ).

Data on wasps collected from the field indicated that the mean number of eggs found in ovarioles for *P. grossa* and *P. thisbe* was 11.3 and 8.4, respectively (Table 1),

with a range of 6–14 and 3–12. Because wasps require a host for each egg, and number of previous encounters with a spider was unknown, the number of eggs produced by each species of wasp prior to any hunting experience could not be determined from field data. However, I have reared both species of wasps from larvae feeding on *A. steindachneri* females (mean weight:  $9.89 \pm 0.61$  g) in the laboratory and found that non-mated *P. grossa* (10–12 days of age) produced 9–21 eggs/female (mean:  $16.2 \pm 3.2$  g SE,  $n = 78$ ) as compared to 4–14 (mean:  $10.2 \pm 2.2$ ,  $n = 38$ ) for *P. thisbe* ( $t = 7.09$ ,  $P < 0.05$ ) (Punzo, unpubl. data).

For all observed encounters between *P. grossa* or *P. thisbe* and a host spider, wasps entered an occupied burrow by cutting through the silk covering over the burrow entrance and then forced the host to the surface. Attack and paralysis never occurred within the burrow. A wasp would typically approach the entrance of a spider burrow and tap its antennae along the edge of the opening. The time allocated by these wasps for each behavioral component of hunting behavior is shown in Table 2.

*Pepsis thisbe* females required significantly more time to complete the overall hunting sequence as compared to *P. grossa* ( $F = 19.27$ ,  $P < 0.05$ ) (Table 2). No significant interspecific differences were found for eviction behavior (EVB; Scheffe  $F$ ,  $P > 0.50$ ) or moving away and grooming (MG1, MG2,  $P > 0.60$ ). Interspecific differ-

Table 2. Time (in min) allocated by females of *Pepsis grossa* ( $n = 54$ ) and *P. thisbe* ( $n = 42$ ) for various behavioral components of the overall hunting sequence during encounters with a host spider, *Aphonopelma steindachneri*. Data are expressed as means; numbers in parentheses represent  $\pm$ SE. Values in rows followed by a different letter are statistically significant ( $P < 0.05$ ). BA (burrow antennation); EVB (eviction behavior); AA (approach and antennation); MG1, MG2 (moving away and grooming); AP (antennation and paralysis); LB (lapping behavior); BO (burial and oviposition); BC (burrow closure).

Behavioral component	<i>Pepsis grossa</i>	<i>Pepsis thisbe</i>
BA	4.8a (0.8)	7.6b (1.1)
EVB	3.4a (0.3)	3.9a (0.4)
AA	8.3a (1.7)	5.1b (0.8)
MG1	4.6a (0.4)	5.2a (0.3)
AP	1.8a (0.2)	2.3a (0.5)
MG2	3.2a (0.6)	2.9a (0.3)
LB <sup>1</sup>	3.6a (1.1)	5.1b (1.8)
BO <sup>2</sup>	14.4a (3.5)	23.2b (4.6)
BC	57.3a (7.1)	73.8b (6.9)
Total:	101.4a	129.1b

<sup>1</sup>Lapping behavior occurred in 18 of 54 encounters for *P. grossa* (33.3%), and in 11 of 42 encounters for *P. thisbe* (26.2%).

<sup>2</sup>Represents data for situations in which a spider was buried in its own burrow.

ences for all other behavioral components were significant. As compared to *P. grossa*, *P. thisbe* females allocated significantly more time for burrow antennation (BA; Scheffe  $F = 6.2$ ,  $P < 0.05$ ), drinking behavior (DB;  $F = 4.9$ ,  $P < 0.05$ ), burial and oviposition (BO;  $F = 7.1$ ,  $P < 0.05$ ), and burrow closure (BC;  $F = 6.9$ ,  $P < 0.05$ ), and significantly less time for approach and antennation (AA;  $F = 5.5$ ,  $P < 0.05$ ).

Wasps of both species approached spiders that they had forced out of their burrows and then tapped the spider's body surface with their antennae. Antennae of *P. grossa* and *P. thisbe* initially made contact with the tarsus of one of the spider's forelegs in 50 of 54 (92.5%) and 39 of 42 (92.8%) encounters, respectively. In other cases, the antennae initially made contact with one of the spider's palps. Subsequently, wasps of both species used their

antennae to explore the lateral region of a spider's cephalothorax and abdomen. During antennation by *P. grossa*, 34 of 54 spiders (63%) exhibited no bodily movements as compared to similar values observed for *P. thisbe* (28 of 42, 67%,  $P > 0.60$ ). For encounters with *P. grossa*, other spiders either remained stationary but exhibited slight movements of their foreleg ( $n = 2$ , 4%) or an elevation of the palps ( $n = 6$ , 11%), while the remainder ( $n = 12$ , 22%) exhibited a threat posture. Comparable values for similar responses of spiders to *P. thisbe* were 5% ( $n = 2$ ), 9% ( $n = 4$ ), and 19% ( $n = 8$ ), respectively. In no case did a spider attempt to flee back into its burrow or attack the wasp, and wasps 'won' all observed encounters.

When initiating attack, wasps of both species showed a preference for grasping leg 3 or 4 of the spider (Table 3). Eight-one and 57% of *P. grossa* and *P. thisbe*, respectively, exhibited a rapid dash under the ventral region of the spider and used their mandibles to grasp leg 3 or 4 before attempting to insert their sting. Leg 1 was never grasped, and leg 2 in only 2.4–7.4% of encounters.

Sting insertion sites for *P. grossa* and *P. thisbe* are shown in Fig. 1. Examination of spiders post-paralysis showed that 78% of *P. grossa* females inserted their sting into the intersegmental membrane between the sternum and coxa 2 of the spider, and 22% between the sternum and pedipalp. In comparison, 88 and 12% of *P. thisbe* females, respectively, inserted their sting into the membrane between the sternum and coxa 1 or at the junction between the abdomen and cephalothorax. Mean time that elapsed between insertion of sting and immobilization (paralysis) of spider (indicated by curling of the legs under the spider's body) was  $6.2 \pm 0.4$  SE (range: 4–8 s) for *P. grossa* and  $12.8 \pm 1.1$  SE (range: 8–16 s) for *P. thisbe*. Regardless of insertion site, there was no significant difference in time required for paralysis for either species of wasp.



Table 3. Leg of spider (*Aphonopelma steindachneri*) grasped by females of *Pepsis grossa* and *Pepsis thisbe* when initiating attack. Data derived from a single observation of each wasp/spider encounter for 54 and 42 encounters, respectively, between *P. grossa* and *P. thisbe*, and a host spider. Spider legs on right and left side of the body (based on position of spider when a wasp was facing it) are designated as R and L, respectively, and legs are numbered 1 (forelegs) through 4 (hindlegs). Values in parentheses represent frequency of occurrence (%).

Spider leg grasped	<i>Pepsis grossa</i> (n = 54)	<i>Pepsis thisbe</i> (n = 42)
R1	0	0
L1	0	0
R2	4 (7.4)	1 (2.4)
L2	0	1 (2.4)
R3	20 (37)	14 (33.3)
L3	24 (44.4)	10 (23.8)
R4	4 (7.4)	7 (16.6)
L4	2 (3.7)	9 (21.4)

Only 33.3 and 26.2% of *P. grossa* and *P. thisbe* females, respectively, exhibited drinking behavior (DB, Table 2). Eleven of 18 (61%) females of *P. grossa* were observed to drink fluid oozing from the wound site (sting insertion site), while 7 (39%) wasps drank fluids from the spider's mouth cavity. For *P. thisbe*, the percentage of females that engaged in DB was 8 of 11 (73%) and 3 of 11 (27%) for the wound site and mouth cavity, respectively.

## DISCUSSION

Physical dimensions and number of eggs for *P. grossa* and *P. thisbe* were similar to values reported for other species of *Pepsis* wasps of similar size. For example, eggs of *P. cerberus* Lucas and *P. mexicana* Lucas from another area of BBNP ranged from 4.19–4.29 and 4.25 vs. 4.31 mm (length), 1.26–1.38 and 1.18–1.29 mm (width), and 7.18–7.32 and 7.06–7.17 g (weight), respectively (Punzo 2005c). In like manner, number of eggs produced per female for *P. grossa* and *P. thisbe* were similar to values reported for other *Pepsis* wasps which range from 2–44/female (Haupt 1952, Evans and West-Eberhard 1970, Punzo 2000, 2005c). It has been shown that the

number of eggs produced by *Pepsis* females (Evans 1953, Punzo 2005c), as well as in many other insects (Price 1975, Ito 1980, Nation 2002) is positively correlated with body size.

Although a majority of paralyzed spiders found with an attached *Pepsis* egg (where encounters with a wasp had not been observed) contained female spiders (68%), almost 1/3 contained a male. Thus, it appears that *Pepsis* wasps are opportunistic hunters and will readily attack a male tarantula even though males are usually smaller than females. This is in general agreement with previous laboratory or field observations showing that *Pepsis* wasps will attack, paralyze, and deposit an egg on male and female theraphosid hosts (Kurczewski and Kurczewski 1968, Punzo 2000). An experimental protocol that might allow us to determine whether female *Pepsis* wasps have any 'preference' for spiders of different sexes would be to observe the response of mated female wasps when given a choice between a male and female spider. If naïve females are used (no previous *Pepsis* encounter with a spider), one can also assess whether such a preference, if exhibited, had an innate component.

Little information is available on the number of eggs produced per female for *Pepsis* wasps. A previous study yielded some data for pepsine wasps collected from Persimmon Gap, a site 48 km to the northeast of TF that also lies within BBNP (Punzo 2005c). Number of eggs in ovarioles from wasps collected immediately after mating (before they started to hunt for hosts) ranged from 5–26 (mean:  $12.7 \pm 2.8$  SE) and 4–20 (mean:  $11.8 \pm 1.7$ ) eggs per female, for *P. cerberus* and *P. mexicana*, respectively. It is difficult to extrapolate and compare these data with values reported for *P. grossa* (11.3) and *P. thisbe* (8.4) in the present study because there was no way of knowing how many prior encounters these wasps had with a host before they were collected. These compare

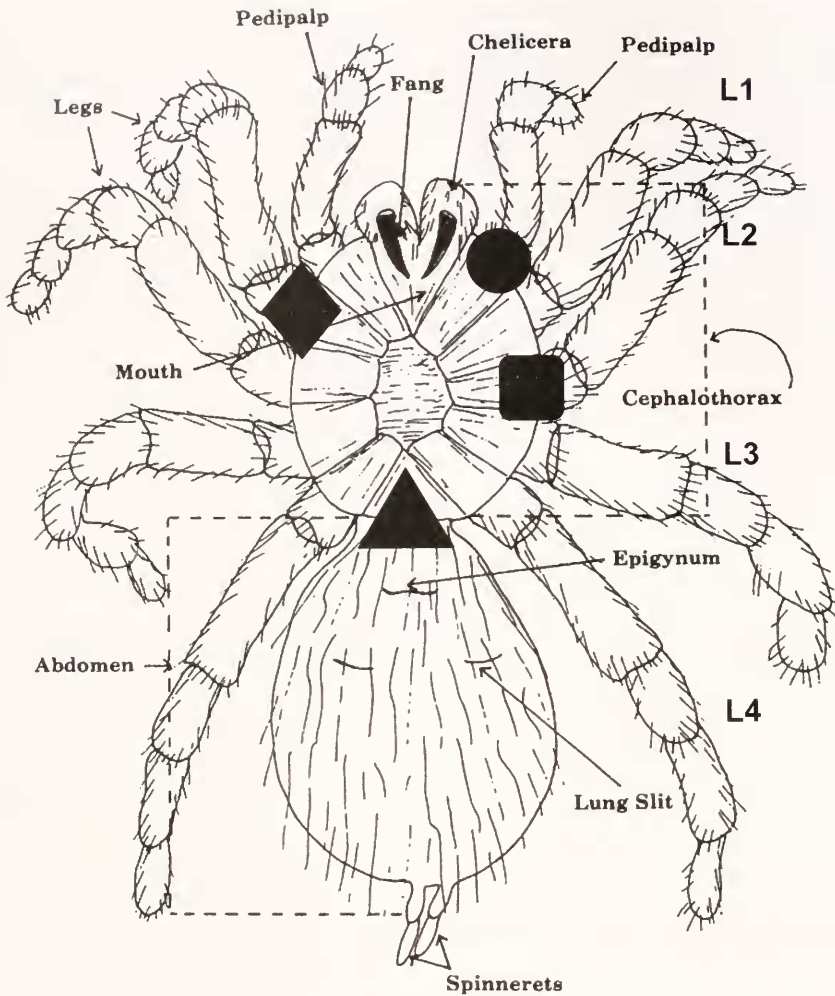


Fig. 1. Ventral body region of *Aphonopelma steindachneri* showing insertion sites (wound sites) for the sting of *Pepsis grossa* and *P. thisbe*. Solid circle and square (intersegmental membrane between sternum and pedipalp, and sternum and coxa 2, respectively) are insertion sites for *P. grossa*; solid triangle and diamond (membrane between sternum and coxa 1, and at junction of cephalothorax and abdomen, respectively) are insertion sites for *P. thisbe*. Legs: L1–L4.

to 9–21 eggs for *P. grossa* and 4–14 for *P. thisbe* reared in the laboratory (Punzo, unpubl. data).

Spiders paralyzed by *P. grossa* and *P. thisbe* varied in body weight. Previous research has demonstrated that adult size (as assessed by head capsule width, length of legs or wings) attained by other species of spider wasps is positively correlated with the mass attained by their last-instar larvae (Vinson 1984, Punzo 2005c), which in turn is positively correlated with the

mass of the spider that the larvae fed on (Price 1997, Punzo 2005c). This most likely accounts for the ranges in adult size observed in male and female *Pepsis* wasps in the field. Although empirical evidence is lacking, it would be interesting to determine to what extent (if any) a decision made by a female *Pepsis* wasp concerning size of host suitable for attack may be influenced by the wasp's size.

There are relatively few detailed observations and analyses on foraging (Cazier



and Mortenson 1964, Punzo and Ludwig 2005, Punzo 2006a,b), territoriality (Rau and Rau 1918, Punzo 2000), dispersal (Evans and West-Eberhard 1970), diel periodicity (Punzo 2005c), and hunting behavior (Petrunkevitch 1952, Williams 1956, Punzo 2005a) in *Pepsis* wasps under natural conditions. Although many aspects of overall hunting behavior for wasps of this genus are similar across species, the results of this field study indicate that there is some interspecific variation associated with certain behavioral components of hunting between *P. grossa* and *P. thisbe* which include frequency of drinking behavior and sting insertion sites. At the Tornillo Flat (TF) study site, females of both species approached a burrow occupied by adult females of *A. steindachneri* and tapped their antennae along the edges of the opening (burrow antennation, BA). Wasps then entered the burrow after cutting through the silk covering and forced the spider out onto the ground surface (eviction behavior, EVB). These behaviors have been reported for encounters between theraphosid spiders and other species of *Pepsis* wasps (Buckley 1862, Petrunkevitch 1926, 1952, Passmore 1936, Punzo 2005a), as well as *P. grossa* (as *formosa*) (Punzo and Garman 1989, Punzo 1991) and *P. thisbe* (Punzo 1994b), that were staged in the laboratory.

Because *A. steindachneri* is the only species of theraphosid spider known to occur at TF, all females of *P. grossa* and *P. thisbe* utilized this species as a host for their larvae. At sites 25–80 km to the north, these two species of wasps, along with *P. mildei* Stål, are known to utilize both sexes of two other theraphosids, *Aphonopelma* (as *Rhechostica*) *hentzi* and *Dugesia* (as *Aphonopelma*) *echina* Hentzi as a host (Punzo and Garman 1989, Punzo 1991). In southern Texas (Hidalgo County), *P. grossa* (as *formosa*) utilizes both sexes of the theraphosids *A. harlingenum* (Chamberlin) and *A. heterops* (Chamberlin) as hosts, although it shows a strong preference for *A. harlin-*

*genum* (Punzo 2006b). Farther to the west, in Arizona and California, *P. grossa* is known to hunt another theraphosid, *A. chalcodes* (Chamberlin) (Cazier and Mortenson 1964). In southern California, *P. thisbe* hunts two theraphosid species, *A. reversum* Simon and *Eurypelma* (as *Aphonopelma*) *eutylum* (Ausserer) (Williams 1956). From the same region, *P. mildei* has been reported to utilize females of the trapdoor spider *Bothriocyrtum californicum* (Chamberlin and Ivie) (Passmore 1933), a mygalomorph spider from an entirely different family (Ctenizidae). However, I have never found a nest containing any species of paralyzed trapdoor spider with a *Pepsis* larvae, or egg at any of a number of locations in BBNP or Big Bend Ranch State Park (Presidio Co., Texas) (Punzo unpubl. data).

These various host records suggest that *Pepsis* wasps have the ability to utilize immatures and adult males and females of a variety of theraphosid spiders as hosts, depending on the theraphosids available at any particular site. Presumably, during the course of evolution in pompilid wasps, selection favored a preference for hunting a single, larger host for each wasp larva. Many species of spider wasps in this genus are among the largest wasps in the New World (Hurd 1952, Vardy 2000, 2002) and adults develop from larvae that attain lengths in excess of 27 mm and can weigh over 5 g (Punzo 2000). In order for a female to provide an adequate amount of food for such large larvae, each larvae would have to be provided with a high number of smaller hosts either together or over a continuous period of time (*progressive provisioning*) as opposed to providing all required food at one time (a single large host or multiple small ones, e.g. by *Trypoxylon* wasps) at one time (*mass provisioning*) (O'Neill 2001). There are obvious trade-offs that are involved. Progressive provisioning involving several smaller prey would require more energy and increase exposure of wasps to potential

predators, while requiring more handling time but less risk from the prey. In contrast, a single, larger, more formidable host, may require less handling time but pose a higher risk from the prey, whilst requiring less overall energy expenditure and a decreased probability of encountering a predator.

The data collected to do not point to specific niche divisions between *P. grossa* and *P. thisbe* at the TF site. I did not observe any significant interspecific differences in the sex or size of spiders selected, nor in temporal patterns of hunting activity. Adult wasps of both species begin to emerge from their nests during late March and continue to do so until August. Females of both species were observed hunting during daylight and evening hours. At sites further south (Zapata Co., Texas), *P. thisbe* begins to emerge in mid-March, whereas *P. grossa* adults are not seen until mid-April (F. Punzo unpubl. data). Perhaps host spiders occurred at sufficiently high densities during the course of the present study at the TF site so that any need for resource partitioning was reduced.

Future studies should further analyze host preference in *Pepsis* wasps. For example, at locations where a *Pepsis* wasp is known to utilize more than one theraphosid species, it would be instructive to assess any differences that may occur with respect to duration of embryonic development, larval growth rate and number of larval instars, size of emerging adults, adult longevity, fecundity, flight endurance, and host preference, for wasps developing on different hosts.

Overall hunting behavior of *Pepsis* wasps (*P. grossa*, *P. thisbe*, *P. mildei*, *P. marginata*, and *Pompilus* spp.) can be categorized into several distinct behavioral components (Table 2), one of which may or may not occur (DB) (Petrunkevitch 1926, Passmore 1936, Evans 1953). These behavioral components were traditionally interpreted as examples of genetically-determined, inflexible acts referred to a fixed action patterns,

FAPs, which are characteristic of instinctive (innate) behavior (Tinbergen 1951). More recent studies, based on sequential laboratory-staged contests between *Pepsis* wasps and spiders, have shown that the amount of time required to perform some behavioral acts decreases as a function of increasing number of encounters (experience) (Punzo and Garman 1989, Punzo, 1991, 2005a).

The term 'modal action pattern' (MAP) has been used to describe components of innate behavior that exhibit some degree of plasticity (Barlow 1977). The acts that have been shown to improve with experience include initial approach and antennation (AA) and attack and paralysis (AP) (Table 2), while the time required for other behavioral components does not. This suggests that some degree of learning is associated with hunting behavior in these wasps (Punzo 1996). It is interesting to note that those acts which a wasp can perform more quickly with experience are precisely those which present the most risk for a wasp. AA requires that a wasp approach within a close distance of the spider and actually touch the spider's body with its antennae, placing it well within the strike distance of the spider (Punzo 2007b). AP requires the wasp to move directly under a spider's body, often passing directly below its fangs, grasp a leg, and insert its sting. In contrast, performance of behavioral acts that pose no risk because the spider has already been immobilized (MG2), or are most likely subject to biomechanical constraints (BO, and BC), do not 'improve' with experience (Punzo 1991, 1994b). Similarly, MG1, which increases the distance between protagonists and thereby decreases risk for a wasp, is not performed more rapidly with increasing number of encounters (Punzo and Garman 1989, Punzo 2000).

During attack, these wasps showed a marked preference for grasping legs 3 or 4 of a spider before stinging it. Perhaps the positions of legs 3 and 4, relative to the

center of gravity for a spider, make it easier for a wasp to obtain the leverage required to insert its sting through an appropriate site on the spider's ventral surface in the least amount of time. The faster a wasp insert its sting the more rapidly it can immobilize a formidable host and reduce the probability of retaliation by the spider. Experiments where a wasp is presented with a spider whose legs 3 or 4 have been removed, would force a wasp to grasp leg 1 or 2, or refuse to attack at all, and would provide a way to assess any possible biomechanical advantage associated with grasping various legs.

All observations of encounters between *Pepsis* wasps and theraphosids have shown that a wasp's sting is directed into the ventral body region of a spider (Punzo 2007b, and references cited therein). Females of *P. grossa* and *P. thisbe* showed a marked preference when choosing a site on the spider's body in which to insert their sting. Little information is available for sting insertion sites for *Pepsis* wasps. Petrunkevitch (1926) observed a female of *P. marginata* insert her sting between the third and fourth right coxae when attacking the theraphosid, *Cyrtopholis portoricae* Simon. Another wasp inserted its sting into the intersegmental membrane between the sternum, maxilla and coxa 1. In an encounter with the theraphosid *Dugesia hentzi*, a *Pepsis* wasp of undetermined species inserted its sting through the membrane between coxa 3 and coxa 4 (Baerg 1958).

The site preferred by females of *P. grossa* and *P. thisbe* was the intersegmental membrane between coxa 2 and sternum, and between coxa 1 and sternum, respectively. These, as well as the other sting insertion sites observed in this study (membrane between pedipalp and sternum, *P. grossa*; junction between abdomen and cephalothorax, *P. thisbe*), all allow a wasp to deliver its venom into the prosomal nerve mass which supplies motoneurons to muscles involved in movements of all legs, chelicerae, and fangs (Foelix 1996, Punzo 2007b).

Some investigators have observed instances in which a wasp failed to locate an insertion site during its first attack on a spider, moved a short distance away, and then attacked again, successfully paralyzing its host (Petrunkevitch 1952, Williams 1956, Baerg 1958). Nonetheless, once the sting delivers venom into the prosomal nerve mass, paralysis of the spider occurs very rapidly as indicated by a curling of the spider's legs under its body, slight twitching movements of some appendages, and then complete immobilization (Petrunkevitch 1926, Cazier and Mortenson 1964, Punzo 2000).

These results on sting insertion sites also indicate that there is behavioral variation exhibited by these wasps. This suggests several interesting questions that future studies should address: do individual wasps choose the same insertion site for all encounters, or do they vary? If sting insertion sites are 'fixed' for individual females this would suggest that the behavioral program has a genetic basis (innate). If so, breeding experiments involving males with females showing different behavioral phenotypes might shed some light on the patterns of inheritance involved in this behavior. Secondly, is there a relationship between a particular insertion site and time required to immobilize a spider?

Nutritional state (body condition) may afford a possible explanation for why drinking behavior (DB) occurs in only some encounters. Drinking hemolymph oozing from a host's wound site may provide necessary nutrients to meet the energetic demands of flight which wasps engage in when searching for hosts, as well as those of venom production, handling time, and burrow closure. Drinking fluids from a spider's mouth cavity may help wasps to maintain proper water balance of body fluids. Similar behavior has been reported for species in other wasp families. For example, Tinbergen (1972) observed that females of the digger wasp, *Philanthus*



*triangulum* Fabricius, which selectively hunt honeybees, *Apis mellifera* L., press the abdomen of a paralyzed bee through their mandibles and lick up the fluid (nectar) extruded from the bee's mouth. Species of spider wasps from other genera are also known to drink fluids from a host's mouth cavity or wound site (Petrunkevitch 1952, Evans 1953, Williams 1956, Evans and West-Eberhard 1970, Punzo 2000).

It may be that wasps engage in DB only after a certain number of foraging bouts have occurred resulting in a need to replenish nutrients and/or body fluids. Experimental protocols using a tethered flight apparatus should be used in future studies to test this hypothesis. Different female wasps could be subjected to forced flight tests for varying periods of time and then allowed to encounter a host. If the hypothesis is true, wasps that are subjected to longer bouts of flight (and thus expend more energy, and lose more water by evaporation) should be more likely to engage in DB than wasps subjected to flying for shorter periods of time. Such an experimental design would also allow one to determine the amount of flight time required to initiate LB in a particular wasp species.

The confines of a spider's burrow might not provide enough room for a wasp to maneuver in such a way as to effectively administer a sting to its host. This may account for the fact that all wasps observed at the TF site forced a spider out of its burrow and onto the ground surface (eviction behavior, EVB) before attacking their host. Similar EVB has been observed for *Pepsis* wasps presented with tarantulas that have been allowed to excavate burrows within their cages under laboratory conditions (Petrunkevitch 1926, Punzo and Garman 1989, Punzo 1991, 1994b).

Interspecific differences in the amount of time required to complete the overall hunting sequence among *P.grossa* and *P. thisbe* in the field may be associated with

some wasps of either species having had more encounters with hosts than other wasps. It may also reflect genetically-based differences in synaptic events associated with afferent (sensory) neural pathways involved with detection and identification of hosts and/or efferent (motor pathways) involved in the control of bodily movements required for various behavioral acts.

On a final note, theraphosid spiders are typically aggressive and innately strike at arthropods that wander within their prey awareness area (Punzo 2007b). The fact that no spider attempted to seize a wasp suggests that the spider's attack response is somehow inhibited. It has been suggested that these wasps may release some chemical compound(s) or possess chemosensory cues associated with their epicuticle that inhibit spider's from attacking them (Petrunkevitch 1952, Punzo 2000). Petrunkevitch (1926) observed that *P. marginata* from Puerto Rico produced a "pungent odor" when initially making contact with a theraphosid host and argued that the substance responsible for this odor might somehow diminish the aggressiveness of the spider. Others have pointed out that the smooth surface of a wasp's cuticle, combined with its high degree of hardness, makes it difficult for a spider's fangs to penetrate a wasp's integument (Petrunkevitch 1926, Passmore 1936).

It should be pointed out that Petrunkevitch (1926) observed a theraphosid (*Cyrtopholis portoricae* Simon) that unsuccessfully attempted to grasp a female of *P. marginata* Lucas with her fangs as the wasp passed under the spider. Cazier and Mortenson (1964) observed a *Pepsis grossa* (as *formosa*) female entering a burrow occupied by *Aphonopelma* sp., and after a few minutes the spider emerged from its burrow with its anterior two legs wrapped around the wasp and its chelicerae inserted into the wasp's abdomen. Nonetheless, the wasp was able to sting the spider. After being stung, the spider released the wasp which exhibited erratic movements and was un-

able to fly. The spider's right leg was rigidly extended forward, making locomotion awkward. After several minutes, the wasp and spider were placed in a screened plastic container and initially both animals avoided one another. When observed 45 min later, the spider was engaged in eating the wasp. These observations suggest that: (1) cues potentially responsible for inhibiting a spider's strike response may not always be effective (2) varying degrees of effectiveness may be species-specific; or (3) mutations may account for differences in the chemical profile of the wasp's cuticle and certain profiles may be less effective at deterring a spider's strike than others.

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